

# FIRE AND SUCCESSION IN PINYON-JUNIPER WOODLANDS OF THE SAN BERNARDINO MOUNTAINS, CALIFORNIA

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## ABSTRACT

Pinyon-juniper woodlands (*Pinus monophylla*, *Juniperus californica*, *J. occidentalis*) of the San Bernardino Mountains were examined for modern and historical fire patterns, post-fire succession, and changes in mature woodlands under 20th century fire suppression management. Thirty-eight burns consisting mostly of high intensity canopy fires were identified, giving an estimated fire rotation period of 480 years. Burns were primarily colonized by Great Basin sage-scrub (*Purshia tridentata*, *Artemisia tridentata*, *Chrysothamnus nauseosus*) at higher elevations (>2000 m), and a mix of California desert chaparral (*Ceanothus greggii*, *Fremontodendron californicum*) and Great Basin sage-scrub at lower elevations (<2000 m). Chronosequence sampling shows that conifer species were absent on all burns  $\leq 18$  years. Shrubs increased in cover and density for 30–50 years, and were joined by *P. monophylla* recruits 25–40 years after fire. Mature shrubs acting as nurse plants appear to aid in the re-establishment of *P. monophylla* by providing a favorable microclimate for seedling survival and early growth. After 50 years, pinyon-juniper woodland development was phased with a declining shrub layer, ultimately leading to the return of a mature woodland at 100–150 years. Replication of the 1929–1935 California Vegetation Type Map survey shows only minor changes in this forest type under 20th century fire suppression management.

Pinyon pine (*Pinus monophylla*, *P. edulis*) in association with juniper (*Juniperus* spp.) occupies approximately 17 million ha in semi-arid western North America (Wright and Bailey 1982). The pinyon-juniper association typically forms open to moderately dense stands with understories of perennial grass in Arizona and New Mexico (Jameson 1962; Dwyer and Pieper 1967), sage-scrub and upland sclerophyll shrub complexes in the Great Basin and Colorado Plateau (Erdman 1970; Tueller et al. 1979; Everett and Koniak 1981), and sage-scrub and desert chaparral in California (Andre et al. 1965; Vasek and Thorne 1988).

Fire patterns and post-fire succession have been documented for much of the pinyon-juniper range, and two generalized fire and succession models have been identified: 1) surface fires with rapid post-fire perennial grass succession, and 2) canopy fires with slow post-fire shrub and tree succession. Perennial grass surface fires in pinyon-juniper woodlands result in light to moderate pinyon-juniper mortality and recovery to pre-fire conditions in <5 years (Jameson 1962; Dwyer and Pieper 1967), whereas pinyon-juniper woodlands

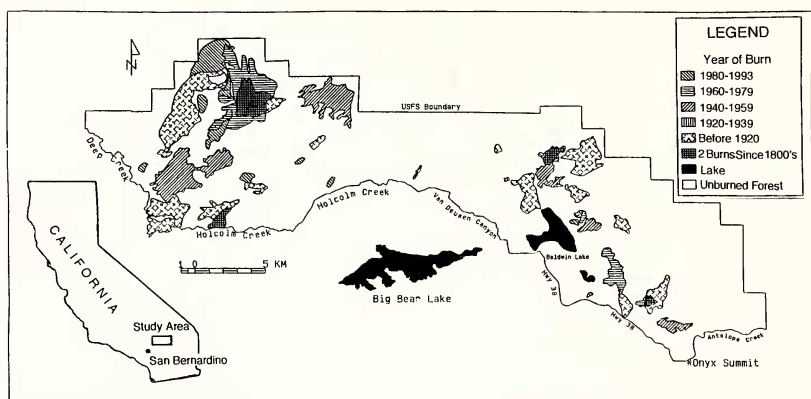


FIG. 1. Fire mosaic map for pinyon-juniper woodlands of the San Bernardino Mountains.

with sage-scrub and upland sclerophyll shrub understories commonly experience canopy fires that result in heavy pinyon-juniper mortality and >100 years for recovery to pre-fire conditions (Erdman 1970; Everett and Ward 1984; Koniak 1985).

In California, pinyon-juniper woodlands have received only cursory attention (Vasek and Thorne 1988), and the fire ecology of these woodlands has not been studied. The objective of this paper is to use a combination of temporal and spatial data from aerial photographs and field methods (chronosequence sampling, replication of the 1929–1935 California Vegetation Type Map survey) to examine the dynamics of fire and succession in pinyon-juniper woodlands of the San Bernardino Mountains in southern California. It is hypothesized that 1) pinyon-juniper woodlands experience canopy fires that result in heavy pinyon-juniper mortality; 2) post-fire succession is slow, beginning with a shrub phase that is slowly invaded by young trees, and eventually replaced by a mature woodland with a sparse understory in 100–150 years; 3) *Pinus monophylla* is dependent on perennial nurse shrubs for successful establishment during post-fire succession.

#### STUDY AREA

California's pinyon-juniper woodlands (*P. monophylla*, *Juniperus californica*, *J. occidentalis*) are widespread along the leeward escarpments of the Sierra Nevada, Transverse and Peninsular Ranges (Griffin and Critchfield 1976), including the San Bernardino Mountains, which are located north-east of the city of San Bernardino (Fig. 1). Pinyon-juniper woodlands occupy approximately 87,000 ha within the San Bernardino Mountains between 1300 and 2700 m

elevation along the semi-arid northern and eastern flanks of the range. Regional climate is mediterranean with winter precipitation and summer drought. Orographic effects result in strong rainshadows in the pinyon-juniper range with mean annual precipitation of 25–40 cm (U.S. Dept. of Commerce 1987).

*Pinus monophylla* is the dominant tree in pinyon-juniper woodlands of the San Bernardino Mountains, forming nearly monotypic stands that are sometimes mixed with California juniper (*J. californica*, <2000 m) and western juniper (*J. occidentalis*, >2000 m). Low elevation (<2000 m) woodland understories consist mostly of desert chaparral (*Ceanothus greggii*, *Fremontodendron californicum*, *Quercus wislizenii*, *Arctostaphylos glauca*, *Cercocarpus betuloides*), while at high altitudes (>2000 m), these woodlands grow with Great Basin sage-scrub (*Artemisia tridentata*, *Chrysothamnus nauseosus*, *Purshia tridentata*), as well as *Quercus chrysolepis* and *Cercocarpus ledifolius* (Minnich 1988). Herbaceous cover is sparse at all elevations as warm season moisture is limited by summer drought.

#### METHODS

*Fire history reconstruction.* With sequential aerial photographs it is possible to follow vegetation change and fire history over time (Minnich, in press; Minnich and Bahre 1995). Pinyon-juniper woodland fires leave visible scars on the landscape that persist >50 years (Minnich 1988), allowing for accurate fire history reconstruction back to the 19th century. Fire history and vegetation change were interpreted in two steps using repeat aerial photographs from 1938 and 1983. 1) stereoscopic viewing, aided by mirror and hand held stereoscopes for coverages on prints, and a Bausch and Lomb roll-film stereoscope with 3× and 8× magnification for coverages on original negative rollfilm. Burn scars were easily recognized on aerial photographs because the removal of vegetation produces a visible contrast between bare, reflective soil and surrounding unburned vegetation. Burn scars were dated back to 1911 by matching them with fire perimeter data on file with the San Bernardino National Forest. 2) Scale matching of site-specific, repeat aerial photographs from 1938 and 1983, using a Bausch and Lomb Zoom Transfer Scope (ZTS). The ZTS permitted observation of two time-series site specific scenes visually superimposed on one another. The same vegetation features in a scene, including burns, were matched exactly from unique stand configurations, as well as from surrounding fixed features such as rock outcrops and watercourses. ZTS registration permitted the examination of post-fire succession between aerial photographs, as well as spatial and temporal changes in stand structure.

*Post-fire succession.* Post-fire succession was estimated by sampling burns along a chronosequence. This permits spatial vegetation patterns to be used as a surrogate for temporal vegetation change in landscapes where age is the only ecologically significant difference among sampling sites (Jackson et al. 1988; Johnson and Gutsell 1994). Twenty-three burns dating back to the 19th century were sampled between August and November, 1993. The sites were located from burn scars recorded on aerial photographs. At each site, shrub cover was estimated with a 100 m line intercept (Bauer 1943), on level or gently sloping terrain at least 100 m inside the burn perimeter. Shrub density was estimated with the point-center quarter method (Cottam and Curtis 1956), using points at 10 m intervals along the intercept. Tree density was estimated at each site with a 100 m  $\times$  10 m belt transect (Lindsey 1956). The sites were divided into two elevational categories,  $>2000$  m and  $>2000$  m, to capture intersite variations due to floristic differences with altitude. Since only burn scars after 1911 could be assigned ages, it was necessary to estimate ages of older burns from their successional status. Ages of 7 undated burns (visible on 1938 aerial photographs) were estimated by obtaining tree ring counts of 10 large (old) *P. monophylla* recruits, and adding 25–40 years based on average recruitment time lags for *P. monophylla* at chronosequence sites with known ages.

Past research has indicated that perennial nurse shrubs play a vital role in the survival of *P. monophylla* recruits following fire (Erdman 1970; Everett and Ward 1984; Koniak 1985). To establish *P. monophylla* dependence on nurse shrubs, a nearest-shrub analysis of *P. monophylla* saplings was conducted. A 10  $\times$  100 m sampling area was established at each of 4 burned sites with abundant saplings. The distance of 51 saplings (estimated age, 5–30 years) was measured to the base of the nearest shrub. Stems  $<5$  years that are highly susceptible to mortality were not counted (Meagher 1943). Sapling/nurse shrub distances were compared with mean inter-shrub distances from point-center quarter data to test for randomness in inter-shrub distances.

*Changes in mature woodlands.* In 1993, twenty-one California Vegetation Type Map (VTM) survey plots, sampled from 1929–1935, were replicated for changes in tree density and size class over a 60 year period (original VTM data on file with Dr. Barbara Allen-Diaz, Department of Forest Resources and Management, University of California, Berkeley). Within a 10 by 80 meter quadrat, trees were counted by species and dbh size class (4–11.9" = 12–33 cm; 12–23.9" = 34–67 cm;  $>24$ " =  $>68$  cm; after Minnich et al. 1995). Since the original VTM quadrats could be located only from map locations within ca. 0.5 ha, three randomly located replications were



conducted at each site, and an average was taken for a t-test comparison with the original data.

## RESULTS

*Fire and succession.* Thirty-eight burns, covering an estimated 15,000 ha, were found in *Pinus monophylla* woodlands of the San Bernardino Mountains (Fig. 1). Approximately 17% of *P. monophylla* woodlands have burned since 1911 giving an estimated fire cycle period, or the time for the total burn area to equal total vegetation area (87,000 ha, Johnson and Gutsell 1994), of 480 years. Two general fire patterns were identified: 1) Canopy fires carried by mature *P. monophylla* woodlands (34 burns, ca. 13,750 ha); 2) Fires carried by mature post-fire shrub canopies that consume post-fire *P. monophylla* recruits (4 burns, ca. 1250 ha). All fires produced a charred landscape of standing dead trees, interspersed with small islands of unburned vegetation.

At elevations <2000 m, a shrub phase persists for ca. 50 years, followed by the slow recolonization of *P. monophylla*. Burns <10 years had resprouts of *Purshia tridentata*, and seedlings of *Artemisia tridentata*, *Chrysothamnus nauseosus*, *Ceanothus greggii*, and *Fremontodendron californicum*. These shrubs dominated throughout the shrub phase (Table 1). The shrubs *Eriodictyon trichocalyx*, *Sphaeralcea ambigua*, and *Gutierrezia microcephala*, formed sparse cover on young burns, but were absent from burns >15 years, persisting only in disturbed sites or rocky areas. Other rare species included *Malacothamnus fremontii*, *Eriogonum fasciculatum*, *Ephedra viridis*, and *Prunus fasciculata*. Total shrub cover and density increased steadily with time-since-fire (8.3% and 1988 stems  $\text{ha}^{-1}$  at 1 year, 18.5% and 6925 stems  $\text{ha}^{-1}$  at 8 years, and 30.2% and 7693 stems  $\text{ha}^{-1}$  at 18 years). Cover and density peaked at 40.5% and 11,339 stems  $\text{ha}^{-1}$  at 47 years (Figs. 2, 3).

*Pinus monophylla* was absent from all burns  $\leq 18$  years, and was infrequent (40–140 stems  $\text{ha}^{-1}$ ) on burns 33–90 years (Table 3). Stand densities were >250 stems  $\text{ha}^{-1}$  on burns  $\geq 130$  years. On burns >47 years, total shrub cover and density decreased rapidly from 21.4% and 7670 stems  $\text{ha}^{-1}$  at 90 years, to 6.3% and 1215 stems  $\text{ha}^{-1}$  at 160 years (Figs. 2, 3). *Pinus monophylla* density increased from 170 stems  $\text{ha}^{-1}$  at 90 years, to 360 stems  $\text{ha}^{-1}$  at 160 years (Table 3). Although skeletons of *C. greggii* and *F. californicum* were often seen, living stems were absent on burns >47 years. *Prunus fasciculata*, *A. tridentata*, and *Purshia tridentata* were the only shrubs consistently found on burns >90 years.

Post-fire recovery on burns >2000 m was similar to that at lower elevations. Burns  $\leq 14$  years were dominated by seedlings of *G. microcephala*, *S. ambigua*, *E. trichocalyx*, as well as *A. tridentata*

TABLE 1. ESTIMATED SHRUB COVER (%) AND DENSITY (STEMS HA<sup>-1</sup>) ON BURNED SITES < 2000 M ELEVATION.)

Species	Years since fire											
	1	8	9	13	18	33	38	47	90*	130*	140*	160*
Estimated cover												
<i>Artemisia tridentata</i>	1.3	3.1	1.9	4.2	9.5	4.3	19.3	17.4	6.5	6.2	3.7	4.6
<i>Ceanothus greggii</i>	1.7	3.5	11.1	10.3	13.1	10.3	3.7	3.4	—	—	—	—
<i>Chrysothamnus nauseosus</i>	0.7	1.7	3.2	3.2	2.6	8.3	1.2	5.2	2.7	—	0.6	—
<i>Ephedra viridis</i>	—	—	—	—	—	—	—	1.6	—	1.1	0.4	—
<i>Eriodictyon trichocalyx</i>	—	1.5	2.9	—	—	—	2.9	—	2.3	—	—	—
<i>Eriogonum fasciculatum</i>	—	—	—	1.3	1.0	—	—	—	1.8	—	—	—
<i>Fremontodendron californicum</i>	—	2.1	6.5	3.3	3.2	3.5	1.1	3.2	—	—	—	—
<i>Gutierrezia microcephala</i>	—	1.2	—	—	—	—	1.5	2.1	0.7	—	—	—
<i>Malacothamnus fremontii</i>	4.6	—	—	—	—	—	—	—	—	—	—	—
<i>Prunus fasciculata</i>	—	—	—	—	—	—	—	2.7	—	—	1.2	—
<i>Purshia tridentata</i>	—	4.7	—	—	0.8	0.7	—	4.2	6.1	2.5	1.6	1.7
<i>Sphaeralcea ambigua</i>	—	0.7	—	2.1	—	—	—	0.7	1.3	—	—	—
Total	8.3	18.5	25.6	24.4	30.2	27.1	29.7	40.5	21.4	9.8	7.5	6.3
Estimated density												
<i>Artemisia tridentata</i>	398	557	336	1564	2439	2174	8711	3849	2314	2050	1312	972
<i>Ceanothus greggii</i>	299	3098	2449	1810	3232	4094	1523	2250	—	—	—	—
<i>Chrysothamnus nauseosus</i>	199	278	995	844	969	4711	1523	1313	1017	—	94	—
<i>Ephedra viridis</i>	—	—	—	—	—	—	—	566	—	153	47	—
<i>Eriodictyon trichocalyx</i>	—	811	1836	—	—	—	1523	—	1473	—	—	—
<i>Eriogonum fasciculatum</i>	—	—	—	564	242	—	—	—	933	—	—	—
<i>Fremontodendron californicum</i>	—	556	1026	422	484	1754	508	1022	—	—	—	—
<i>Gutierrezia microcephala</i>	—	202	—	—	—	—	508	783	311	—	—	—
<i>Malacothamnus fremontii</i>	1092	—	—	—	—	—	—	—	—	—	—	—
<i>Prunus fasciculata</i>	—	1221	—	—	—	—	—	632	—	—	280	—
<i>Purshia tridentata</i>	—	202	—	—	327	313	—	783	1311	153	140	243
<i>Sphaeralcea ambigua</i>	—	—	—	422	—	—	—	141	311	—	—	—
Total	1988	6925	6642	5626	7693	13,046	14,296	11,339	7670	2356	1873	1215

\* Estimated burn ages dated from tree cores.

$$\bigcirc < 2000 \text{ m}; y = 11.98 + 1.12x - .02x^2 + 5.93E-5x^3; r^2 = .865$$

$$\blacksquare > 2000 \text{ m}; y = -8.87 + 2.59x - .04x^2 + 1.54E-4x^3; r^2 = .919$$

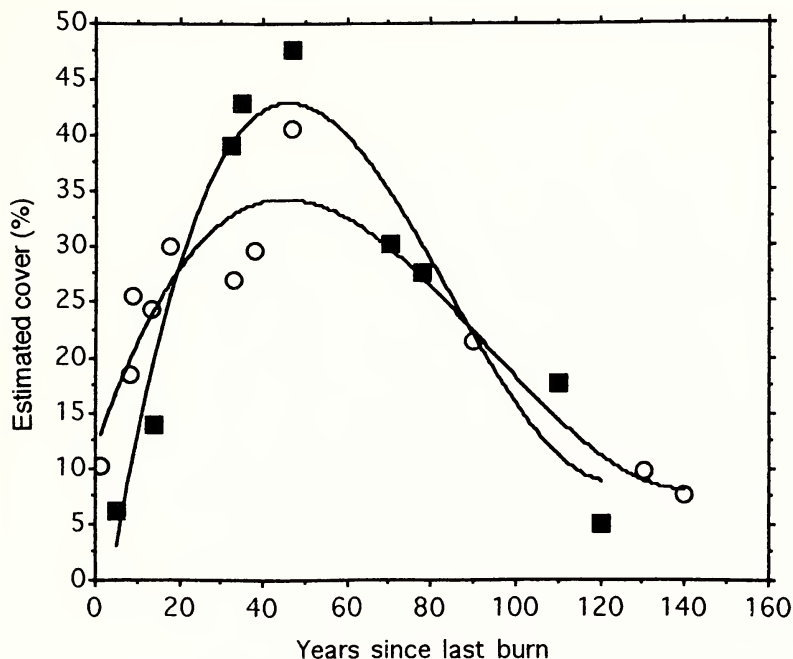


FIG. 2. Third order polynomial regressions for total shrub cover (%) on chronosequence sites.

and *C. nauseosus*. The dominant resprouters were *P. tridentata* and *E. viridis*. *A. tridentata* and *C. nauseosus* co-dominated on burns <30 years, with *A. tridentata* becoming solely dominant on burns >40 years (Table 2). Total shrub cover and density increased to 39.1% and 14,375 stems  $\text{ha}^{-1}$  at 32 years (Figs. 2, 3), and maintained maximum levels of 38.2–47.7% and 12,063–16,199 stems  $\text{ha}^{-1}$  at 32–47 years.

*Pinus monophylla* was absent from burns  $\leq 35$  years, but was present on all burns  $\geq 47$  years (Table 3). *Pinus monophylla* density varied from 80 stems  $\text{ha}^{-1}$  at 47 years to 544 stems  $\text{ha}^{-1}$  at 160 years. Total shrub cover and density decreased from 30.0% and 10,423 stems  $\text{ha}^{-1}$  at 70 years, to 17.6% and 3968 stems  $\text{ha}^{-1}$  at 110 years (Figs. 2, 3). *Pinus monophylla* density increased from 180 stems  $\text{ha}^{-1}$  at 70 years, to 404 stems  $\text{ha}^{-1}$  at 110 years (Table 3). At 120–160 years, total shrub cover and density decreased to 5.8–6.2% and 1343–1423 stems  $\text{ha}^{-1}$ , and *P. monophylla* density increased to

$$\bigcirc < 2000 \text{ m; } y = 1631.43 + 545.73x - 7.89x^2 + .03x^3; r^2 = .923$$

$$\blacksquare > 2000 \text{ m; } y = -2224.98 + 873.49x - 13.36x^2 + .05x^3; r^2 = .951$$

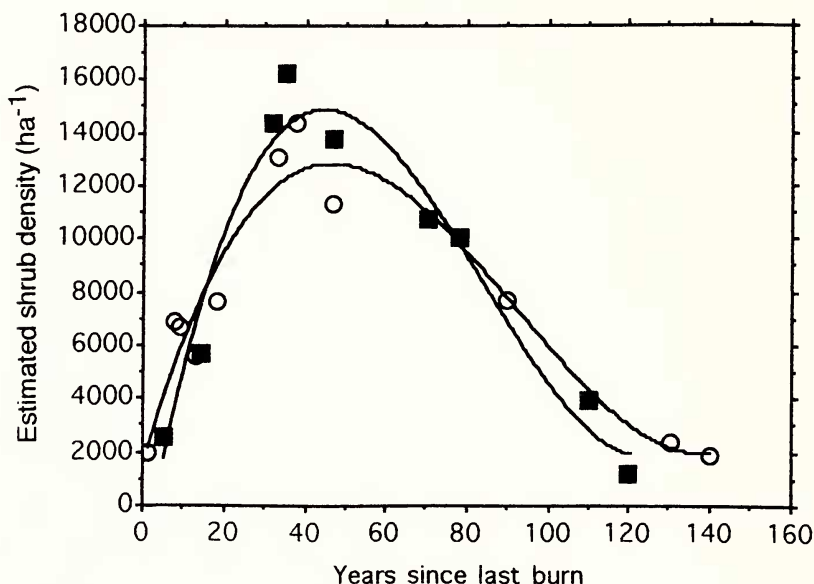


FIG. 3. Third order polynomial regressions for total shrub density ( $\text{ha}^{-1}$ ) on chronosequence sites.

451–544 stems  $\text{ha}^{-1}$ . *Chrysothamnus nauseosus* was rare on burns >47 years and *A. tridentata* formed only sparse cover on burns >70 years. *Cercocarpus ledifolius*, a nonsprouter, established sparingly on burns >47 years, and persisted on burns  $\geq 78$  years along with *Amelanchier utahensis*, *E. viridis*, *A. tridentata* and *P. tridentata*.

At all sites, *P. monophylla* saplings were commonly seen emerging through shrub canopies with stems located near shrub root axes. Ninety percent of the saplings were rooted within 26 cm of the nearest shrub root axis, with 50% of individuals  $\leq 5$  cm (Fig. 4). Perennial nurse shrubs consisted primarily of *A. tridentata*, *C. nauseosus*, *F. californicum*, and *C. greggii*. The mean inter-shrub distance for all sites was 114 cm.

*Mature woodlands.* Original data from the 1929–1935 VTM field quadrats show that pinyon-juniper woodlands consisted of open to moderately dense stands with a relatively open shrub understory dominated by *A. tridentata*, *Cercocarpus ledifolius*, and *C. betuloides* (Table 4), similar to modern old growth stands (Tables 1–3). *Pinus monophylla* formed mixed-aged woodlands that varied in den-

TABLE 2. ESTIMATED SHRUB COVER (%) AND DENSITY (STEMS HA<sup>-1</sup>) ON BURNED SITES >2000 M ELEVATION.

Species	Years since fire										
	5	14	32	35	43	47	70	78	110*	120*	160*
<b>Estimated cover</b>											
<i>Anelanchier utahensis</i>	—	—	—	—	—	—	—	—	1.4	—	—
<i>Arctostaphylos patula</i>	—	—	—	—	—	—	10.7	—	—	—	—
<i>Artemisia tridentata</i>	—	2.1	18.4	22.3	19.3	19.1	14.6	4.2	10.3	3.2	3.7
<i>Ceanothus greggii</i>	—	1.4	—	—	—	11.4	—	—	—	—	—
<i>Cercocarpus ledifolius</i>	—	—	—	—	5.1	—	—	1.3	—	0.8	—
<i>Chrysothamnus nauseosus</i>	1.1	3.0	12.1	12.1	7.2	6.1	—	—	0.8	—	—
<i>Ephedra viridis</i>	0.9	0.4	—	1.5	1.8	—	—	7.7	—	—	—
<i>Eriodictyon trichocalyx</i>	—	2.6	—	—	3.2	4.4	2.1	—	—	—	—
<i>Fremontodendron californicum</i>	—	—	—	—	—	6.7	2.6	—	—	—	—
<i>Gutierrezia microcephala</i>	0.6	—	1.1	1.2	—	—	—	1.2	—	—	0.4
<i>Purshia tridentata</i>	2.2	4.5	5.3	3.6	1.6	—	—	13.2	4.5	1.8	2.1
<i>Sphaeralcea ambigua</i>	3.6	—	2.2	2.3	—	—	—	—	0.6	—	—
<b>Total</b>	<b>8.4</b>	<b>14.0</b>	<b>39.1</b>	<b>43.0</b>	<b>38.2</b>	<b>47.7</b>	<b>30.0</b>	<b>27.6</b>	<b>17.6</b>	<b>5.8</b>	<b>6.2</b>
<b>Estimated density</b>											
<i>Anelanchier utahensis</i>	—	—	—	—	—	—	—	—	199	—	—
<i>Arctostaphylos patula</i>	—	—	—	—	—	—	1416	—	—	—	—
<i>Artemisia tridentata</i>	—	638	7531	7822	5142	6302	6411	1293	2074	980	875
<i>Ceanothus greggii</i>	—	638	—	—	—	2342	—	—	—	—	—
<i>Cercocarpus ledifolius</i>	—	—	—	—	1872	—	—	258	—	121	—
<i>Chrysothamnus nauseosus</i>	515	2208	4907	6091	3021	2278	—	—	399	—	—
<i>Ephedra viridis</i>	192	159	—	—	624	—	—	2328	399	—	—
<i>Eriodictyon trichocalyx</i>	—	319	—	—	780	2342	1631	—	—	—	—
<i>Fremontodendron californicum</i>	—	—	—	—	—	468	965	—	—	—	—
<i>Gutierrezia microcephala</i>	192	—	176	228	—	—	—	258	—	—	110
<i>Purshia tridentata</i>	1143	1753	1509	1602	624	—	—	3879	698	242	438
<i>Sphaeralcea ambigua</i>	515	—	252	456	—	—	—	—	199	—	—
<b>Total</b>	<b>2557</b>	<b>5715</b>	<b>14,375</b>	<b>16,199</b>	<b>12,063</b>	<b>13,732</b>	<b>10,423</b>	<b>8016</b>	<b>3968</b>	<b>1343</b>	<b>1423</b>

\* Estimated burn ages dated from tree cores.



TABLE 3. ESTIMATED TREE DENSITIES (STEMS HA<sup>-1</sup>) ON BURNED SITES.

Species	Years since fire											
	1	8	9	13	18	33	38	47	90*	130*	140*	160*
<2000 meters elevation												
<i>Juniperus californica</i>	—	—	—	—	—	—	—	—	30	—	—	—
<i>Pinus monophylla</i>	—	—	—	—	—	60	150	40	140	320	273	360
Total	0	0	0	0	0	60	150	40	170	320	273	360
	Years since fire											
Species	5	14	32	35	43	47	70	78	110*	120*	160*	
>2000 meters elevation												
<i>Juniperus occidentalis</i>	—	—	—	—	—	40	30	10	18	24	—	
<i>Pinus jeffreyi</i>	—	—	—	—	30	10	—	—	—	—	—	
<i>Pinus monophylla</i>	—	—	—	—	—	80	180	110	404	451	544	
Total	0	0	0	0	30	130	210	120	422	475	544	

\* Estimated burn ages dated from tree cores.

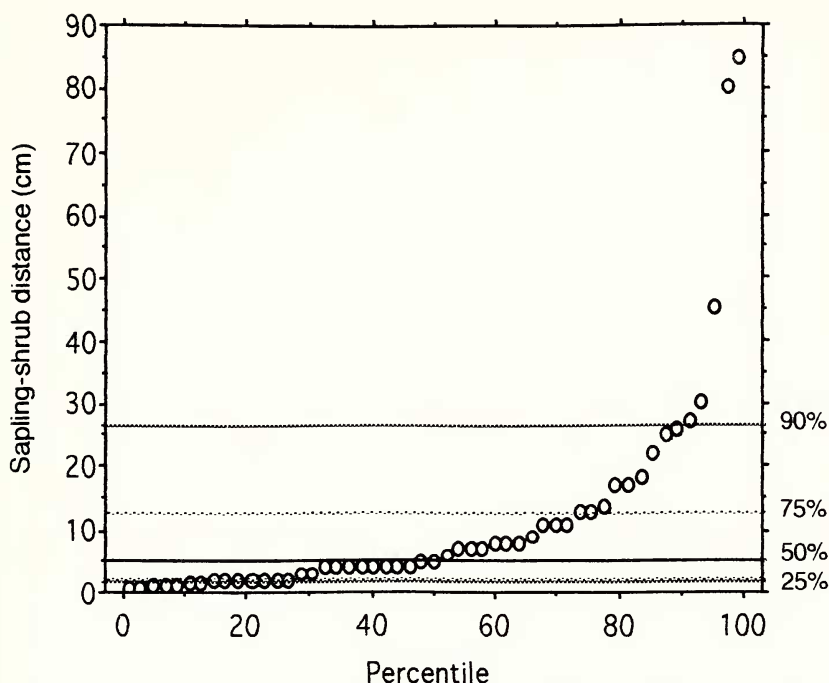


FIG. 4. Cumulative frequency graph for *P. monophylla* sapling-nearest shrub analysis.

sity from 50 to 450 stems  $\text{ha}^{-1}$  with an average of  $192.3 \pm 24.5$  stems  $\text{ha}^{-1}$  (Fig. 5a). Eighty percent of stems, averaging  $155.4 \pm 21.3$  stems  $\text{ha}^{-1}$ , had dbh's  $< 33$  cm, while most remaining trees had dbh's of 34–67 cm. Few trees exceeded 67 cm. *Juniperus occidentalis* density ranged from 0 to 62 stems  $\text{ha}^{-1}$  (average,  $8.9 \pm 4.1$   $\text{ha}^{-1}$ ), with most stems falling in the 34–67 cm size class (average,  $5.4 \pm 3.1$  stems  $\text{ha}^{-1}$ , Fig. 6a).

Replication of VTM plots in 1993 show that modern *P. monophylla* stand density ranges from 75 to 475 stems  $\text{ha}^{-1}$  with an average of  $220.8 \pm 26.1$  stems  $\text{ha}^{-1}$  (Fig. 5b), an insignificant increase of 15% since 1929–1935 ( $P > 0.05$ ,  $\text{df} = 20$ , Table 5). Average stand density for dbh  $< 33$  cm did not change significantly ( $P > 0.05$ ,  $\text{df} = 20$ ), but did increase significantly for dbh 34–67 cm ( $P \leq 0.05$ ,  $\text{df} = 20$ ). Few trees exceed 67 cm. Modern *Juniperus occidentalis* density ranges from 0 to 50 stems  $\text{ha}^{-1}$  with an average of  $9.5 \pm 3.5$  stems  $\text{ha}^{-1}$  (Fig. 6), an insignificant increase of 6% ( $P > 0.05$ ,  $\text{df} = 20$ , Table 6). Size classes underwent little change.

#### DISCUSSION

The fire regime of pinyon-juniper woodlands in the San Bernardino Mountains is dominated by long-period canopy fires and slow

TABLE 4. SHRUB COVER (%) AS REPORTED BY 1929-1935 VTM SURVEY FOR PINYON-JUNIPER WOODLANDS.

Plot #	Altitude (m)	Ag	Ap	Apn	Atr	Cg	Cb	Cl	Fc	Pi	Qc	Qcm	Qw	Total
Deep Creek Zone														
B-1-14	1189	5	—	—	—	6	10	—	—	6	—	—	—	27
B-1-15	1265	7	—	—	—	6	11	—	1	—	—	—	6	31
B-2-9*	1615	—	—	—	24	21	9	—	15	—	—	—	—	69
B-3-2	1783	—	—	—	—	—	—	—	—	—	—	—	—	0
B-3-3	1753	—	—	—	12	—	—	—	—	—	—	—	—	12
B-3-11	1814	—	—	—	2	1	—	—	—	—	—	—	—	3
B-3-14	1814	—	—	—	41	—	—	—	—	—	—	—	—	41
B-3-15	1768	—	—	—	6	3	3	—	1	—	—	—	—	13
B-3-17	2012	—	—	—	3	—	—	22	—	—	42	—	—	67
B-3-18*	2286	—	4	—	7	34	—	—	13	—	16	—	—	74
C-1-10	1341	—	—	—	—	7	16	—	—	—	—	—	12	35
C-2-9	1448	—	—	—	—	2	12	—	—	—	—	—	—	14
C-2-10	1570	—	—	—	—	—	3	—	4	—	1	—	—	8
C-2-12	1387	—	—	—	—	4	5	—	7	—	—	—	—	16
C-3-1	1798	—	—	—	9	2	9	—	—	—	—	—	—	20
C-3-8	1875	—	—	—	—	—	—	—	—	—	—	—	—	0
San Gorgonio Zone														
B-3-1	1890	—	—	—	—	—	—	8	—	—	—	—	—	8
C-2-6*	2286	—	2	—	14	22	—	25	2	—	—	—	—	65
C-2-8	2423	—	—	—	—	—	—	5	—	—	—	—	—	5
C-2-9	2286	—	—	—	—	—	—	6	—	—	—	—	—	6
C-2-10	2377	—	9	—	—	—	—	12	—	—	—	—	—	21
C-2-11	2225	—	—	—	—	—	—	9	—	—	—	—	—	9
C-2-12	2103	—	—	—	4	—	—	4	—	—	—	—	—	8
C-3-1	1859	—	—	—	19	—	—	—	—	—	—	—	—	19
C-3-4	2072	—	—	—	3	—	—	—	6	—	—	—	—	9
C-3-6	2118	—	—	—	17	—	—	—	—	—	2	—	—	19
C-3-7	2103	—	—	—	17	—	—	—	—	—	—	—	—	17
C-3-9	2164	—	—	—	—	—	—	—	—	—	24	—	—	24
C-3-11	2195	—	—	—	10	—	—	20	3	—	—	—	—	33
C-4-1	1890	—	—	—	—	—	—	—	—	—	—	—	—	0
C-4-2	1981	—	—	—	12	—	—	—	—	—	—	—	—	12
D-3-2	2286	—	—	—	—	—	—	—	1	—	3	—	—	4
D-4-2	2347	—	—	—	1	—	—	7	—	—	—	—	—	8
D-4-4	2195	—	—	—	—	—	—	6	—	—	16	—	—	22
D-4-5	2103	2	—	—	—	—	—	—	—	—	21	—	—	23
D-5-2	1646	—	—	—	—	—	—	—	—	—	—	14	—	14
D-5-3	1951	—	—	—	—	—	—	—	—	—	—	1	—	1
D-5-5	2073	—	—	—	—	—	—	—	—	—	39	—	—	39

\* Sampled within 19th century burn perimeters.

Ag: *Arctostaphylos glauca*; Ap: *Arctostaphylos patula*; Apn: *Arctostaphylos pungens*; Atr: *Artemisia tridentata*; Cg: *Ceanothus greggii*; Cb: *Cercocarpus betuloides*; Cl: *Cercocarpus ledifolius*; Fc: *Fremontodendron californicum*; Pi: *Prunus ilicifolia*; Qc: *Quercus chrysolepis*; Qcm: *Quercus cornelius-mulleri*; Qw: *Quercus wislizenii*.

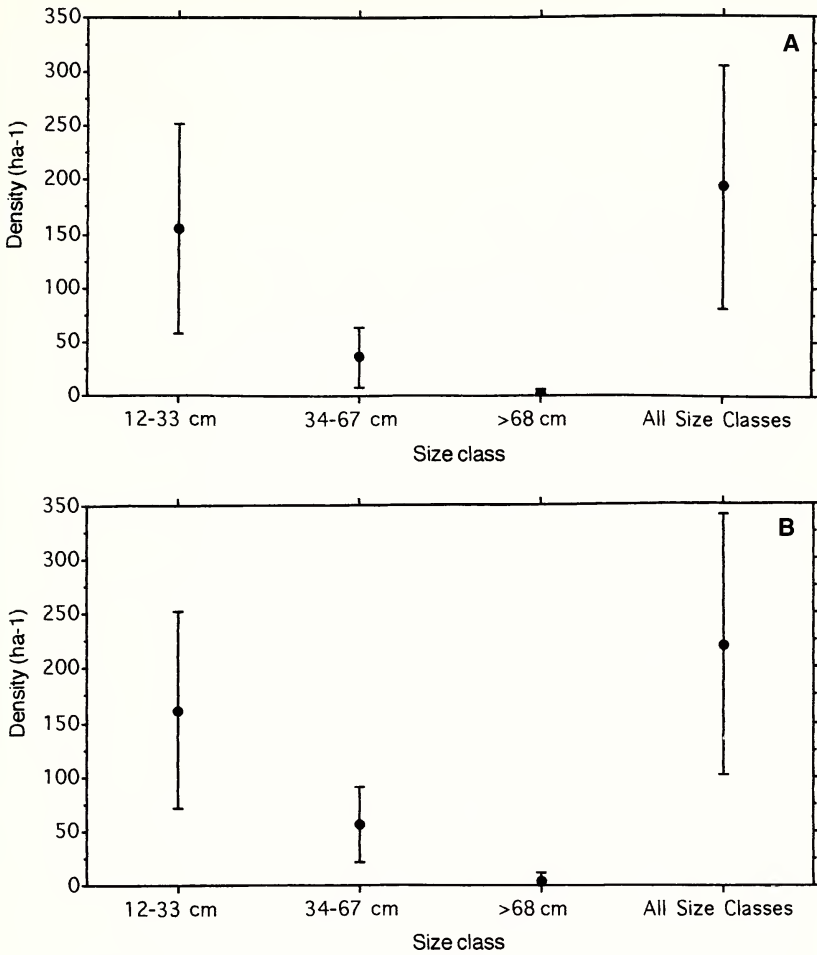


FIG. 5. A) Average *P. monophylla* density by size class for 1929-1935 VTM survey. B) Average *P. monophylla* density by size class for 1993 survey.

post-fire succession. These woodlands are restricted to rain shadows at middle and high altitudes where production of woody fuels, litter and flashy herbaceous cover are limited by cold winters and prolonged warm season drought (Minnich 1988). The open fuel arrangement of stands tends to restrict burns to severe weather (high winds and low relative humidity), resulting in intense stand replacement fires. Tree mortality is high because of pitchy foliage and basal canopies that are contiguous with ground fuels (Minnich 1988). Fires are brief because extreme weather necessary for fire spread is

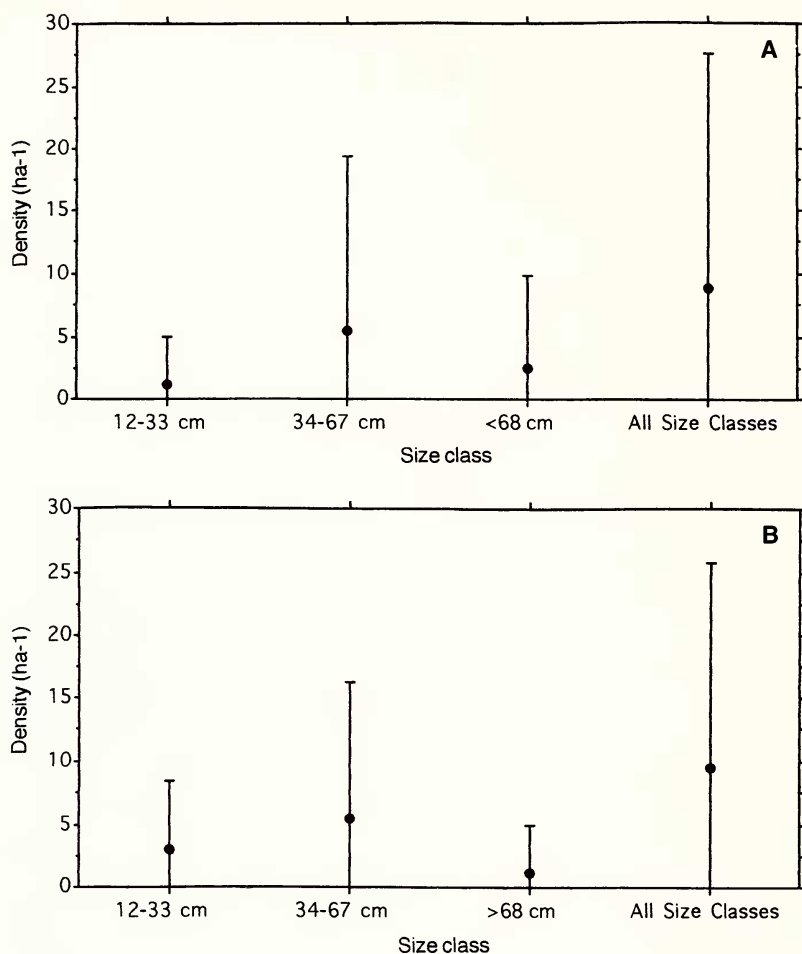


FIG. 6. A) Average *J. occidentalis* density by size class for 1929-1935 VTM survey. B) Average *J. occidentalis* density by size class for 1993 survey.

TABLE 5. COMPARISON OF AVERAGE *PINUS MONOPHYLLA* DENSITY (HA<sup>-1</sup>) BY SIZE-CLASS FOR 1929-1935 VTM SURVEY AND 1993 REPLICATION.

(DBH in cm) size class	(Stems ha <sup>-1</sup> ± standard error)		P value
	1929-1935	1993	
12-33	155.4 ± 21.3	161.3 ± 19.7	0.384
34-67	35.7 ± 6.0	55.9 ± 7.5	0.007
>68	1.2 ± 0.8	3.6 ± 1.8	0.096
All sizes	192.3 ± 24.5	220.8 ± 26.1	0.143



TABLE 6. COMPARISON OF AVERAGE *JUNIPERUS OCCIDENTALIS* DENSITY (HA-1) BY SIZE-CLASS FOR 1929–1935 VTM SURVEY AND 1993 REPLICATION.

(DBH in cm) size class	Stems ha <sup>-1</sup> ± standard error)		P value
	1929–1935	1993	
12–33	1.2 ± 0.8	2.9 ± 1.2	0.076
34–67	5.4 ± 3.1	5.4 ± 2.4	0.493
>68	2.4 ± 1.6	1.2 ± 0.8	0.078
All sizes	8.9 ± 4.1	9.5 ± 3.5	0.431

usually short-lived, resulting in a mosaic of mostly small, scattered patches within uniform old growth stands across the landscape.

Pinyon-juniper succession is characterized by the colonization of opportunistic shrubs into disturbed, mineral soil habitats in full sun as the result of canopy burns. While initial *P. monophylla* recruitment appears to be autogenically dependent on nurse shrubs, the development of mixed-aged stands with canopy closure suggests that nurse shrub dependence eventually ceases in later succession. Canopy closure also causes die-back in most understory shrub species, reducing the probability of short-period understory fires breaching the developing *P. monophylla* woodland.

The shrub phase is dominated by species adapted for efficient colonization of burns (Noble and Slatyer 1980), including re-sprouting (*P. tridentata*, *E. viridis*, pers. obs.), wind-blown seed establishment (*A. tridentata*, *C. nauseosus*, *G. microcephala*, *E. trichocalyx*, *S. ambigua*, Burkhardt and Tisdale 1976), and establishment from *in situ* refractory seed banks (*C. greggii*, *F. californicum*, Keeley 1991). Once established, individual species must rely on longevity and/or the ability to continuously recruit to survive later into succession.

The disappearance of *G. microcephala* and *S. ambigua* in early succession suggests they are short-lived. They persist locally by recruiting continuously on permanently disturbed sites such as washes, road cuts and rock outcrops. *Ceanothus greggii* and *F. californicum* establish even-aged stands from seed banks immediately following fire. *Ceanothus* spp. are known to continuously cache seeds in the soil from the time of reproductive maturity (ca. 5 years) until senescence (usually <50 years) and to germinate only in the presence of ash (Mooney and Miller 1985). Both shrubs disappear after ca. 50 years. These shrubs may also suffer photosynthetic decline in the shade of *P. monopylla* (Campbell 1977). Continuous recruitment of *A. tridentata* and *C. nauseosus* accounts for most of the increase in shrub density during the shrub phase (Tables 1, 2). However, *A. tridentata* and *C. nauseosus* also decline late in succession, forming a discontinuous understory with other shade-tolerant species (*P. tridentata*, *C. ledifolius*) in mature *P. monophylla* woodlands. Al-

though the shrub phase is dominated by desert chaparral (*C. greggii*, *F. californicum*) at lower elevations, and Great Basin sage-scrub (*A. tridentata*, *C. nauseosus*) above 2000 m, total shrub cover and densities are similar across all elevations (Figs. 2, 3).

The establishment of *P. monophylla* after 25–40 years appears to be autogenic as specific environmental conditions may be necessary for successful establishment (Weaver and Clements 1938). Although *P. monophylla* seeds are large and heavy, and do not survive fire directly, establishment during early succession is not limited by dispersal, because jays, nutcrackers, and small mammals such as ground squirrels continuously cache seed (Van der Wall and Balda 1976). Instead, a combination of several environmental factors appear to inhibit early establishment of *P. monophylla*. In early succession, unshaded seedlings are susceptible to mortality from exposure to direct solar radiation. Phillips (1909) observed that *P. monophylla* recruits best in the shade of mature woodlands. Meagher (1943) reported high *P. monophylla* mortality due to insolation on exposed sites one year after germination.

*Pinus monophylla* recruitment may also be deterred by cold nights and frost heaving. Clear windless nights combined with low relative humidities result in rapid nocturnal radiational cooling favorable for ground inversions, with minimum temperatures below freezing between October and May (Minnich 1971). Because snow cover is limited most years (Minnich 1986), seedlings are frequently exposed to frost, and the upper soils to frost heaving which may uproot newly established seedlings. Meagher (1943) reported that frost and frost heaving account for greater seedling mortality on exposed sites than on shaded or shrub covered sites. Indeed, heavy *P. monophylla* seedling mortality was observed at restoration plantings on recent burns east of Baldwin Lake.

*Pinus monophylla* saplings are typically rooted in the shade of mature shrubs, often next to their root axes (Fig. 4). Apparently the shrub canopy provides a regulated microclimate that gives seedlings the best chance for survival. This is supported by average sapling-shrub distances that are an order of magnitude less than mean inter-shrub distances. Above 2000 m, the initial establishment of *P. monophylla* is delayed 10–15 years longer than at lower elevations (Table 3). Still, mature stand densities are greater at high elevations due perhaps to a wetter climate (Fig. 7). Establishment of *Juniperus* spp. is thought to be similar (Meagher 1943), but the low frequency of these trees in the San Bernardino Mountains precluded their examination.

Once *P. monophylla* begins to dominate a site, it appears that the developing tree canopy moderates environmental conditions so that seedlings establish in the shade of older trees without the aid of nurse shrubs. In the field we observed little heaving in mature stands

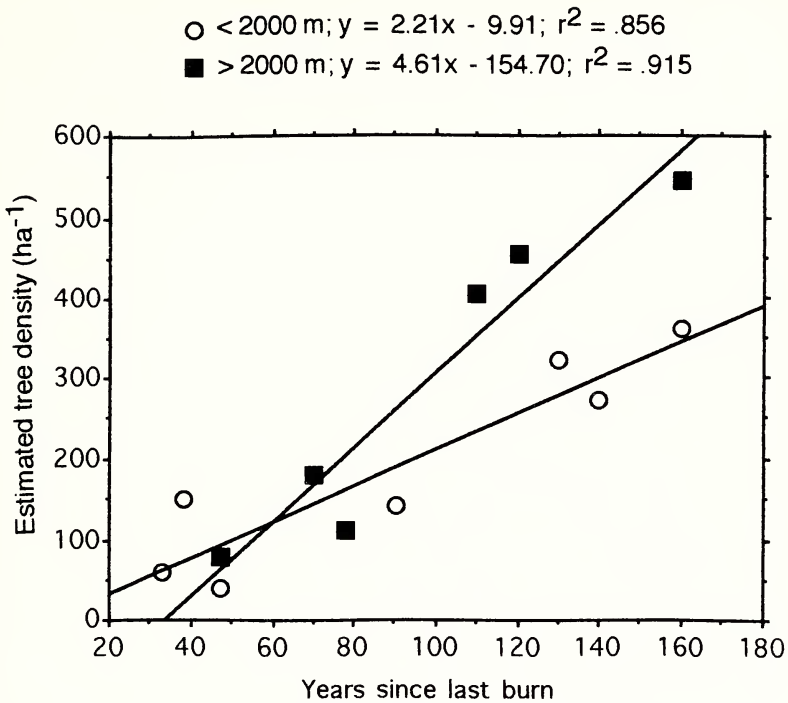


FIG. 7. Linear regressions for total tree density ( $\text{ha}^{-1}$ ) on chronosequence sites.

immediately adjacent to burns where heaving is active. The local change in microclimate is probably related to nocturnal long-wave radiant energy fluxes associated with tree canopies (Miller 1981). During clear, windless nights (ca.  $200 \text{ year}^{-1}$ , Minnich 1971), equivalent downward long-wave radiant fluxes (sky radiation) are  $20\text{--}40^\circ\text{C}$  below ambient (Miller 1981), resulting in intense ground inversions and soil freezing. In mature woodlands, nocturnal ground level air temperatures reflect radiant emissions of tree canopies whose temperatures are close to ambient.

The broad homogeneity of pinyon-juniper woodlands in the San Bernardino Mountains, as indicated by VTM data, suggests that this vegetation type may achieve some old-growth equilibrium in species composition and stand structure. Canopy closure initiates a period of continuous recruitment of *P. monophylla*, as suggested by uneven-aged dbh size distributions. This is typical of white pines which recruit best in shade (Fowells 1965). Stand densities of  $150\text{--}300 \text{ ha}^{-1}$  are achieved by 100 years after fire. Whether densities continue to increase with stand age, or reach some equilibrium between recruitment and mortality is unclear.

*Comparison with pinyon-juniper woodlands in the Southwestern United States.* Fire and succession patterns in pinyon-juniper woodlands of the San Bernardino Mountains are similar to those reported in the Great Basin and Colorado Plateau. In these regions, sparse understories and open tree canopies restrict burning to times of severe weather, resulting in a mosaic of small, stand-replacement burns within a uniform old-growth landscape (Erdman 1970; Everett and Ward 1984; Koniak 1985). Overall productivity is limited by cold winters and low annual precipitation that reduce photosynthetic activity during much of the year (Caldwell, 1985). Post-fire succession begins with a shrub phase that is followed by the gradual establishment of trees in the shade of nurse shrubs. Koniak (1985) recorded conifer establishment in dense stands of Great Basin sage scrub 20–30 years after fire, and reported tree canopies topping the shrub layer 60 years after fire. Erdman (1970) concluded that shrub densities gradually decline in the shade of tree canopies, resulting in mature woodlands with sparse shrub understories 200–300 years after fire.

Studies in Arizona and New Mexico report that pinyon-juniper woodlands with perennial grass understories experience short interval, low intensity fires that cause high mortality among young recruits <2 m tall, but rarely kill mature trees. In Arizona, Jameson (1962) found that young trees <2 m tall accounted for >70% of *J. monosperma* mortality, and in New Mexico, Dwyer and Pieper (1967) reported that all trees <1.5 m tall were fire-killed, but total tree mortalities were only 24% for *J. monosperma* and 13.5% for *P. edulis*. In both regions, perennial grasses (*Bouteloua gracilis* and *B. eriopoda*) resprouted from undamaged root crowns, resulting in rapid recovery of herbaceous biomass within 2 years.

In the San Bernardino Mountains, short-interval surface fires seldom occur due to lack of herbaceous cover, and slow rates of post-fire succession. Understory fires in successional Great Basin sage-scrub and desert chaparral communities result in high mortality among both shrub and tree layers. Fires are usually short-lived, and rarely spread beyond the successional community into adjacent mature pinyon-juniper woodlands. Evidence against short-interval fires is the marginal overlap between contiguous burns. This pattern indicates that stands seldom reburn during early successional stages. Hence, the spread of fire is system-regulated and influenced by previous fire history (Loucks 1970; Heinzelman 1981), similar to chaparral (Minnich 1983, in press).

It is asserted that fire intervals have been lengthened in pinyon-juniper woodlands of the Great Basin and Colorado Plateau during the 20th century due to the combined effects of fire suppression management and removal of herbaceous cover due to heavy livestock grazing (Cottam and Stewart 1940; Johnsen 1962; Arnold et al. 1964; Blackburn and Tueller 1970; Nabi 1978; Tausch et al.

1981; Wright and Bailey 1982). The shift toward longer fire intervals appears to encourage pinyon and juniper expansion in these regions (Arnold et al. 1964; Blackburn and Tueller 1970; Nabi 1978; Tausch et al. 1981; Wright and Bailey 1982). In the San Bernardino Mountains, pinyon-juniper woodlands were grazed in the late 19th and early 20th centuries (Minnich 1988). However, low overall productivity and limited herbaceous cover during the warm season may have mitigated the impact of grazing on fire intervals.

Pinyon-juniper woodlands of the San Bernardino Mountains have remained unchanged since the late 19th century, before fire control was initiated. Past and present fires have been most frequent in mesic stands at the highest elevations, but rare in woodlands adjacent to the Mojave Desert (Leiberg 1899, 1900; Minnich 1988). Leiberg described the pinyon-juniper association as consisting of moderately dense woodlands interspersed with a mosaic of different aged canopy burns across the landscape. Leiberg (1900) saw little evidence of surface fires, reporting that bole scars were noticeably absent. In northern Baja California, Mexico, where little fire intervention exists, pinyon-juniper woodlands also experience long-period canopy fires at intervals of centuries (Minnich in press). Replication of VTM quadrats in the San Bernardino Mountains show that stand densities and size class distributions have experienced only minor changes since 1932. This is in sharp contrast to Californian mixed-conifer forests where pre-suppression forests of open old growth trees of large size classes have shifted to dense stands of shade-tolerant sapling and pole size trees (Vankat 1977; Vankat and Major 1978; Minnich et al. 1995). Moreover, site-specific scale matching of 1938–1983 aerial photographs show that recent stand turnover by canopy burns has been paralleled by recolonization of trees on 19th century burns, and that pinyon-juniper distributions have remained unchanged.

#### CONCLUSION

In the pinyon-juniper woodlands of the San Bernardino Mountains, infrequent canopy fires result in a mosaic of mostly small, scattered patches within uniform old-growth stands across the landscape. Post-fire succession to mature woodlands proceeds over a span of a century, beginning with the colonization of Great Basin sage-scrub (*P. tridentata*, *A. tridentata*, *C. nauseosus*) at higher elevations (>2000 m), and a mix of California desert chaparral (*C. greggii*, *F. californicum*) and Great Basin sage-scrub at lower elevations (>2000 m). The shrub phase increases in cover and density for 30–50 years, and is joined by *P. monophylla* recruits at 25–40 years. Initial recruits appear to be dependent on perennial nurse shrubs which provide a regulated microclimate suitable for *P. mon-*



*ophylla* establishment. After 50 years, increases in *P. monophylla* densities are phased with a decline in the shrub layer, and the development of a self-regulating micro-climate that favors *P. monophylla* recruitment without the aid of nurse shrubs. Mature woodlands with sparse understories return at 100–150 years. Lengthened fire intervals and pinyon-juniper expansion, as reported in the Great Basin and Colorado Plateau, have not occurred in the San Bernardino Mountains, even under fire suppression management.

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